AN APPLICATION OF AN INTEGRATED POPULATION MODEL:

Estimating Population Size of the Fortymile Caribou Herd Using Limited Data

By

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Abstract

An Integrated Population Model (IPM) was employed to estimate the population size of the Fortymile Caribou herd (FCH), utilizing multiple types of biological data. Current population size estimates of the FCH are made by the Alaska Department of Fish and Game (ADF&G) using an aerial photo census technique. Taking aerial photos for the counts requires certain environmental conditions, such as the existence of swarms of mosquitoes that drive the majority of caribou to wide open spaces, as well as favorable weather conditions, which allow low-altitude flying in mid-June. These conditions have not been met in recent years so there is no count estimate for those years. IPMs are considered as alternative methods to estimate a population size. IPMs contain three components: a stochastic component that explains the relationship between biological information and population size; demographic models that derive parameters from independently conducted surveys; and a link between IPM estimates and observed-count estimates. In this paper, we combine census count data, parturition data, calf and female adults survival data, and sex composition data, all of which were collected by ADF&G between 1990 and 2016. During this time period, there were 13 years - including two five-consecutive-year periods - for which no photo census count estimates were available. We estimate the missing counts and the associated uncertainty using a Bayesian IPM. Our case study shows that IPMs are capable of estimating a population size for years with missing count data when we have other biological data. We suggest that sensitivity analyses be done to learn the relationship between amount of data and the accuracy of the estimates.

Key words: Bayesian statistics; population size estimate; integrated model; limited data; Fortymile; caribou.

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1. Introduction

Many different methods and models have been used to estimate wildlife population size. These classical methods include complete census counts, incomplete counts, indirect counts, and mark-recapture methods. Complete counts are used when we know the majority of the population is sited in open areas in certain seasons. These methods can be accurate when performed under ideal conditions, but these conditions are not guaranteed every year. Incomplete counts could be used effectively when we have a strong understanding of population distribution across variable habitats. Incomplete count methods include quadrat sampling, line or point-transect methods, or roadside counts. Indirect counts, on the other hand, are used as indices of relative population size. These include counting feces, nests, or carcasses in certain areas. These counts could be a good indicator of the change in a population size for a species that stays in an area or has known yearly movement patterns, though this method by itself cannot estimate the actual population size. Mark-recapture methods have been used to estimate both fish abundance and game population.

There are a few weaknesses in these classical methods. When there is a year that count data could not be obtained, the missing value is often imputed using other types of data for that year or other years' counts. These point estimates lack flexibility to take into account multiple types of biological or environmental information at the same time, even though short-term population change can be a product of imbalances in multiple demographic processes, such as immigration, emigration, productivity, and survival (Weegman et al., 2016; Pulliam 1998; Watkinson & Sutherland, 1995). Another weakness of the classical methods is that the uncertainty in population growth cannot be measured separately from variances in demographic parameters (Schaub & Abadi, 2011).

An alternative approach, which we utilize in this study, is an Integrated Population Model (IPM), which combines multiple data sources into a unified model (D.J. Tempel et al., 2014; Besbeas et al., 2002; Abadi et al., 2010a) and estimates all the parameters simultaneously, enabling us to estimate parameters even when there is data missing for some years. By fitting the integrated model into a Bayesian framework, we are provided with more flexibility than a frequentist framework without a requirement of normality or linearity (Schaub and Abadi, 2011; Schaub et al., 2007; Brooke et al., 2004). Wildlife managers monitor populations by conducting various surveys to determine population status. Depending on the species and management objectives, the annual monitoring of populations could provide enough information for an IPM. The data from these independent surveys could be limited to certain years, but IPMs have potential to accommodate data collected at irregular intervals.

The Fortymile caribou herd (FCH) has a home range that extends from east-central Alaska, US, to West-central Yukon, Canada. A map is attached as Appendix A-1. FCH was the largest herd in Alaska in the 1920s, with estimates of 568,000 individuals (Murie, 1935; Valkenburg and Davis, 1994). Since then, the herd has experienced large fluctuations in size. By the early 1940s, it is believed that the population size dropped to between 10,000 and 20,000 (Skoog, 1956; Valkenburg and Davis, 1994). In the early 1950s, it increased to 50,000 (Skoog, 1956), and dropped again to 40,000 by 1958 (Olson, 1959). Another major decline occurred between 1960 and 1973 (Valkenburg and Davis, 1994). Some of the conceivable causes were high harvests, unfavorable weather, and high wolf numbers (Valkenburg and Davis, 1994).

Increased effort beginning in the early 1970s has been made by the Alaska Department of Fish and Game (ADF&G) to estimate the population (Valkenburg and Davis, 1994). Aerial photo census techniques have been the main source of population size estimates of FCH since they were introduced in 1973. However, it has been difficult to meet the conditions that aerial photo censuses require. To be able to take photos of the herd, the majority of caribou have to be gathered in open areas. This aggregation may happen when caribou try to avoid mosquito swarms. Mosquito populations and behavior are greatly influenced by temperature and wind. Changes in climate dynamics may impact these mosquito populations, and how they behave impacts photo censuses of caribou. Likewise, the weather must be favorable for low-altitude flying. These conditions have not been present every year, and census count data has been sparse since 2000. In order to estimate population size in years with no aerial photo census estimate, we use an IPM, which utilizes data from years with more data for the estimate.

The objective of this paper is to estimate the population size of FCH from 1990 through 2016, which includes several years with no aerial census count estimates, using an IPM. The rest of the paper is organized as follows. In Section 2, we summarize the types of data available for monitoring the FCH. Section 3 describes our methods, beginning with an illustration of the structure of an IPM, and explains how IPMs work. Then, we describe how we use the data and the prior distribution for each parameter in the model to fit a fully Bayesian model. Section 4 shows the model estimates and compares them with available minimum counts, which were obtained from a photo census. After a brief conclusion, we discuss our results and future work to be considered for further applications.

2. The Fortymile Caribou Herd Data

ADF&G monitors the population status of the FCH using surveys and harvest data. For modeling, ADF&G provided the following data, which was collected between 1990 and 2010. The count data, denoted by y_t, is the total herd population size estimated using aerial photos. The location of caribou in the herd is monitored for several days to examine their aggregation status between mid-June and mid-July. When the caribou are appropriately aggregated, ADF&G conducts the photo-census across the entire summer range in one day (Boertje et al., 2017). Each individual caribou was counted in photos using magnification (10$\times$) under bright lights. Therefore, the counts are lower bounds for the population size.

Productivity was measured by parturition, the pregnancy rate of cows that are 36 months or older. A portion of adult females that were radio collared for a survival study were monitored for the parturition survey. ADF&G observed females of 36 months or older in May to check for the presence of newborn calves, hard antlers, or distended udders. These signs are used as a proxy for the number of calves. Twinning is not common for caribou. These cows ages are known. Female caribou of 24 months or younger are not reproductive. The parturition probability for 36-month-old females depends on the nutrition conditions, whereas those that are 48 months and older have a relatively stable parturition probability (Boertje et al., 2012). Due to modeling decisions, a single estimate of productivity for all reproductive females required combining annual parturition rates for females 36 months and older (1990 through 1992), 36-month-old (1993 through 2016), and 48 months and older (1994 through 2016). Sample sizes of 36 month olds were determined to be inadequate (mean n=9.75 per year); therefore, we combined the data for all ages for this study.

Survival data of adult females that are older than 12-month-old were collected by radio tracking. A total of 638 female caribou were radio collared during September of years 1991 through 2016. The collared animals have been tracked to determine the condition (live, dead, or collar dysfunctional), located at least twice a month in summer and monthly during winter. Those that were collared and died before they turned one year old were removed from adult female survival data, and are included in calf survival study. The data include the unique ID of each individual, the capture date, the last date of known fate, and the status, whether alive or dead. We restructured the data with staggered entry. That is, we have the total number of animals at risk in each summer, which is the number of collared cows that were alive in the summer, and the number of the individuals that survived until at least the following summer. It has not been 12 months since the summer of 2016, and the data is incomplete; therefore, we removed those data. Adult female age is known but we do not utilize adult female age in this research.

Calf survival data was collected in a fashion similar to adult female survival data. A total of 693 calves, including both sexes, were radio collared within a day or two after they were born between May 11th and May 28th in the years from 1994 through 2002. The collared calves were tracked daily in May, every two to three days in June, weekly from July through the end of September, and at least once a month between October and April. The last tracking was done on the 1st of June for calves that were born in the previous year. The data is in a similar format as adult female survival.

Sex composition data was collected on one-day surveys in late September or early October from 1990 through 2015. ADF&G counted cows, calves, and bulls separately along the full extent of the migration each year using radio collared females to locate groups. An effort to correct for bias was made by determining the proportion of radio-collared females in each group. Cows, calves and bulls are known to be less segregated during this survey season than at other times of the year, and there is an assumption that the number of bulls that are not with cows is small enough to be ignored. The data contains corrected bull counts, corrected cow counts, and corrected calf counts. Sex composition data was used to adjust model estimates for males.

3. Method

3.1. Introduction to IPM

We begin by describing the basics of Bayesian IPMs before applying such a model to FCH. IPMs have three basic components: a stochastic part that describes the demographic dynamics (1 in Figure 1), demographic information that include data from independent studies (2), and a link between IPM estimates and observed count data (3) (kéry and Schaub, 2012). We describe each these components in this section, using a simple IPM. I will illustrate with a simple model, where we consider a species that reproduces asexually with first reproduction at age two.

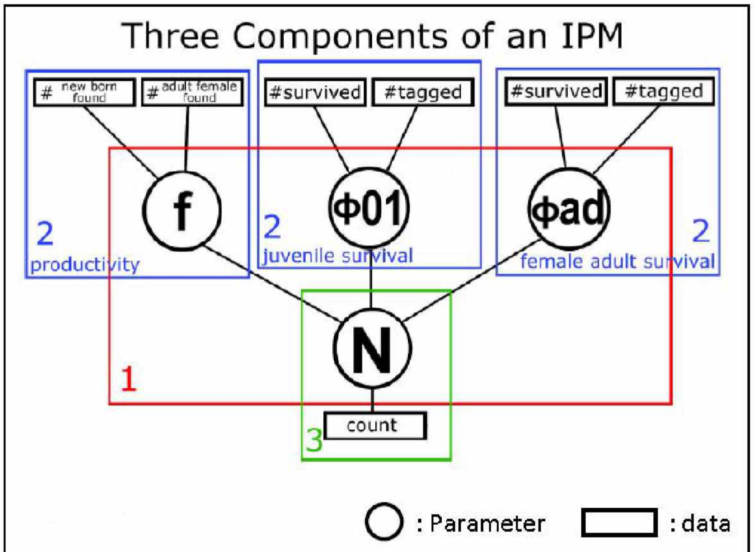

Figure 1.

3.1.1. *Stochastic model*

The first step of constructing an IPM is to develop a demographic dynamics model. Leslie matrix models (Leslie, 1945) are commonly used to describe population growth trends. The relationship among the parameters shown in box 1 in Figure 1 is formalized in a Leslie matrix model. All the parameters in Figure 2 are latent unobserved variables. In particular, N's are state vectors. The population size of a

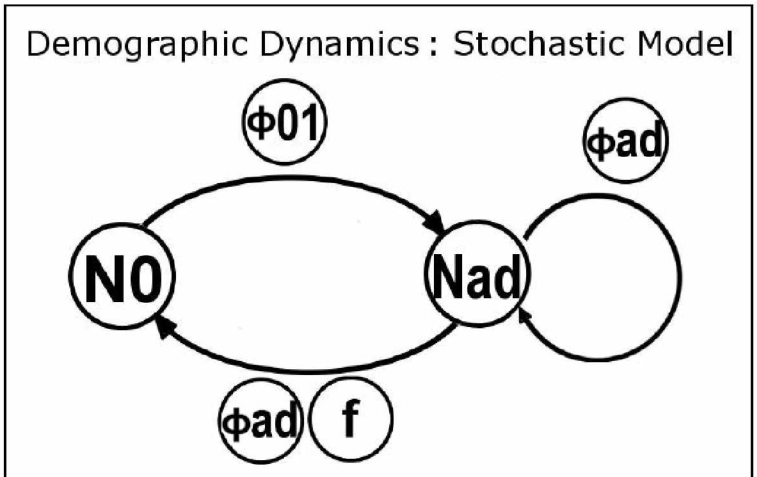

Figure 2.

new generation ($N0_t$) is determined by the adult population in the previous year (Nad_{t-1}), the fraction of them that survived (ϕad_{t-1}) and the average number of offspring (f_t) for each surviving adult female. The population size of adults this year (Nad_t) is determined by the population size of the new generation that was born the year before $N0_{t-1}$), the population size of adults the year before (Nad_{t-1}), and the survival probabilities ($\phi 01_{t-1}$) and (ϕad_{t-1}). In a matrix form these relationships could be described as:

$$\begin{pmatrix} N0 \\ Nad \end{pmatrix}_t = \begin{pmatrix} 0 & \phi ad_{t-1} \cdot f_t \\ \phi 01_{t-1} & \phi ad_{t-1} \end{pmatrix} \begin{pmatrix} N0 \\ Nad \end{pmatrix}_{t-1} \qquad t = \text{year}$$

Unlike Leslie matrix models, which assume all these components are known or given point estimates, IPMs treat the parameters as being unknown, and we model them using probability distributions. This is our state-space model for the simple species we are using as illustration:

$$\mathbb{E}\begin{pmatrix} N0 \\ Nad \end{pmatrix}_t = \begin{pmatrix} 0 & \phi ad_{t-1} \cdot f_t \\ \phi 01_{t-1} & \phi ad_{t-1} \end{pmatrix} \begin{pmatrix} N0 \\ Nad \end{pmatrix}_{t-1} \qquad t = \text{year}$$

For example, $N0_t$ might have a Poisson distribution and Nad_t might have a Binomial distribution.

3.1.2. *Demographic information*

After developing a stochastic model for population size, the next consideration is the estimation of survival and productivity parameters using demographic data from independent studies. This corresponds to the box 2's in Figure 1. Recall that in the Bayesian framework, statistical inference requires assumptions of a prior probability distribution and a likelihood function. The likelihood for survival probabilities (ϕ's) and productivity (f's) utilizes data obtained from independent surveys. Here are three examples that illustrate how one might model survival or productivity:

Survival probability: Each individual animal that is alive in year $t-1$ has a probability of ϕad_{t-1} of being alive 12 months later.

$$\#\text{ alive at year } t \sim \text{Binomial}(\#\text{ at-risk at year } t-1,\, \phi ad_{t-1})$$

Productivity for species that have 0 or 1 offspring per adult: Each adult at year t has a probability f_t of having one offspring.

$$\#\text{ offspring in year } t \sim \text{Binomial}(\#\text{ adult in year } t,\ f_t)$$

Productivity for species whose expected number of offspring is more than the number of adults: Each adult at year t has a mean number f_t of offspring

$$\#\text{offspring at year } t \sim \text{Poisson}(\#\text{ adult at year } t,\ f_t)$$

We assign priors to these parameters using prior knowledge from independent studies. For example:

$$\phi ad_t \sim \text{Beta}(a.ad\ ,\ b.ad)$$
$$f_t \sim \text{Beta}(a.f\ ,\ b.f)$$

The hyperprior parameters($a.ad$, $b.ad$, $a.f$, and $b.f$) are chosen so that the posterior distribution of ϕad_t reflects data without being strongly restricted by the prior distribution. The hyperpriors are chosen based on the characteristics of the parameter. In the example above, a probability of an adult reproducing or a probability of an animal's survival until next year must be somewhere between 0 and 1. In such case, a Beta distribution could be appropriate for ϕ_t or f_t. Setting the shape parameters for the Beta distribution requires knowledge about the animal of interest or previous studies. For instance, f_t could be greater than 1 if one adult produces multiple offspring, but smaller if the number of offspring is fewer than the number of reproducing adults in the Poisson model.

3.1.3. *Integration of the model*

Lastly, there is a link between each state variable $N_t(= N0_t + Nad_t)$ and an observed count y_t, which are used as population indices. Often we assume y_t's are normally distributed, although the link function is chosen based on how the y was observed. For example, if the observed count was the minimum count, N_t should be specified to be greater than or equal to y_t. This is a state-space structure model with a framework that uses different types of data to simultaneously estimate trajectories of population size and parameters. It describes the state of population dynamics such as survival rate and productivity, which is of interest in ecological applications and for management purposes. An IPM allows the use of separately-estimated population sizes, recruitments, survivals and movements from various different data collections whose methods largely depend on the target species. The multi-layer structure of a state-space model allows uncertainty to be divided amongst each level. Other information, such as harvest number or the adjustment in number between seasons of two different surveys, could be included in specific places in the model to improve the accuracy of the estimate.

An IPM integrates the three components described above into one joint model (Figure 1). An IPM is a simulation model that can be used for data generation and estimation. Specific benefits of using an IPM are: 1) when explicit data are not available for some demographic parameters it is still possible to estimate the rate with different datasets contributing to estimates of different model components; 2) there is information about demographic rates both from explicit data on demographic rates and from data on population size, which allows demographic rates to be estimated with reduced observation errors or sampling bias; and 3) a joint analysis allows a comprehensive assessment of the state and the dynamics of a population by extracting information from multiple datasets. A Bayesian IPM gives much flexibility in choosing distributional forms. An IPM is built on the assumption that demographic or counts data sets are independent, which is often not practical with limited resources and budget. Abadi et al. (2010) found that the impact of a violation of this independence assumption on the parameter estimates was minimal.

3.2. Application of IPM to Fortymile Caribou Herd Population Estimation

For FCH, we extend the basic structure described in the previous section. Additional complications are present in the FCH data and must be accounted for in our model. These complications include more than two age groups, sex ratio, and temporal misalignment. They are discussed in the subsections 3.2.1 through 3.2.3. A description of all the parameters is listed on the next page.

Parameters:

parameter	description	years
$N_{0,t}$	Number of female calves born in year t (post-breeding)	1990 – 2016
$N_{1,t}$	Population of 12mo females in year t (post-breeding)	1990 – 2016
$N_{2,t}$	Population of 24mo females in year t (post-breeding)	1990 – 2016
$N_{ad,t}$	Population of females 36mo or older in year t (post-breeding)	1990 – 2016
$N_{tot,t}$	Total (calf + cow + bull) population in year t (post-breeding)	1990 – 2016
λ_t	Population growth rate between year t and year $t+1$	1990 – 2015
$\phi_{01,t}$	Survival probability of the first 12 months of calves born in year t	1990 – 2015
$\phi_{12,t}$	Survival probability of females between 12mo at year t and 24mo at year $t+1$	1990 – 2015
$\phi_{23,t}$	Survival probability of females between 24mo at year t and 36mo at year $t+1$	1990 – 2015
$\phi_{ad,t}$	Survival probability of females 36mo or older between year t and year $t+1$	1990 – 2015
$f_{36,t}$	Fecundity probability of female 36months old at year t	1991 – 2016
$f_{48+,t}$	Fecundity probability of female 48months or older at year t	1991 – 2016
FM_t	[Female 12mo or older]/[Total 12mo or older] at year t	1990 – 2016
σ_y^2	Observation error	

Parameters in hyperpriors:

$a01$ and $b01$	used for prior distribution of $\boldsymbol{\phi_{01}}$
$a.ad$ and $b.ad$	used for prior distribution of $\boldsymbol{\phi_{ad}}$
a and b	used for prior distribution of $\boldsymbol{f}$.
$a.comp$ and $b.comp$	used for prior distribution of $\boldsymbol{FM}$

3.2.1. *Stochastic model*

We outline the population dynamics of female caribou, incorporating the available data sets. The model we consider has a structure as in Figure 3. We make this cycle based on the female population. Accounting for males is discussed in Sections 3.2.2.5 and 3.2.3.

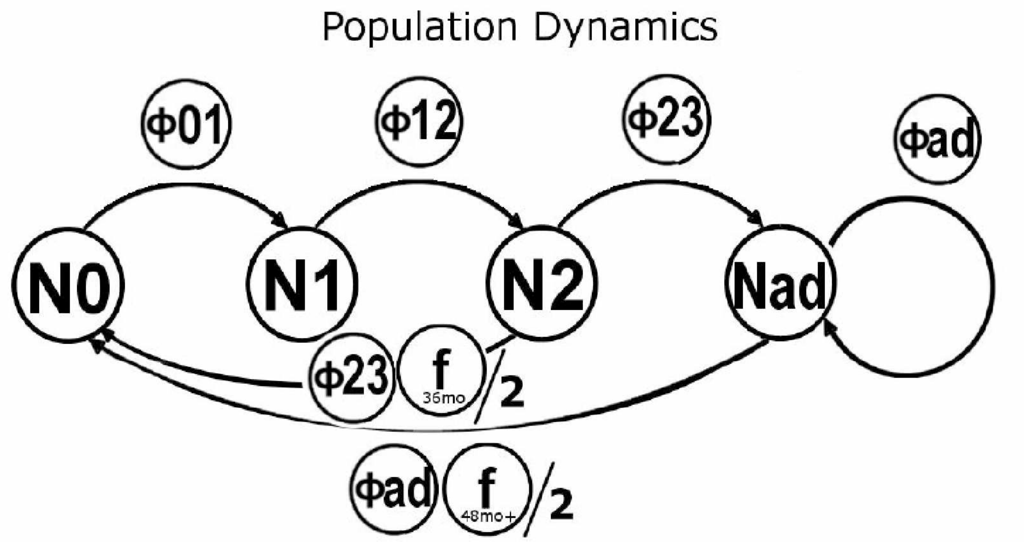

Figure 3.

We set four different parameters for different populations in the herd. N_0 represents the total number of female newborn calves. N_1, N_2, and N_{ad} are the total number of females at age 12 months, 24 months, and 36 months or older, respectively. Parturition probability of 24 months old is very low in Alaska; parturition happens only with extremely good nutritional status, and their calves rarely survive (Boertie and Gardner, 1998). $\phi01$ represents the annual survival probability of females from birth to 12months old. $\phi12$, $\phi23$, and ϕad is the probability of 12months old making it to 24 months old, 24 months old making it to 36 months old, and 36 months old or older living another year, respectively.

Calf survival probability, $\phi01$, is lower than adult survival, therefore N_0 and N_1 have to be separated. N_1, which is the number of 12-month-old females, will not contribute to reproduction in the following summer. The 24-months-old female population, N_2, will reproduce in the following summer if they survive. N_{ad} is the number of females that are 36 months or older which will also reproduce in the following summer if they survive, but they are separated from N_2 because the productivity of N_2 highly depends on the nutrition level whereas N_{ad} has relatively steady productivity. In this study, we fit our model assuming $\phi 12 = \phi 23 = \phi ad$ and $f_{36} = f_{48+}$, due to the available data size of f_{36}; however, estimating these parameters separately by age group would give more information about environmental change, as we explain in the discussion. We assume that the sex ratio of new born calves is 1:1. Thus, the expected number of newborn female calves at year $t+1$ is (the total # of reproductive females at year t)×(their survival probability from year t to $t+1$)×(parturition probability at year $t+1$)/2. The expected population size of each age group can be expressed in a matrix form as follows.

$$\mathbb{E}\begin{pmatrix} N_0 \\ N_1 \\ N_2 \\ N_{ad} \end{pmatrix}_{t+1} = \begin{pmatrix} 0 & 0 & \phi 23_t \cdot \frac{f_{36,t+1}}{2} & \phi ad_t \cdot \frac{f_{48+,t+1}}{2} \\ \phi 01_t & 0 & 0 & 0 \\ 0 & \phi 12_t & 0 & 0 \\ 0 & 0 & \phi 23_t & \phi ad_t \end{pmatrix} \begin{pmatrix} N_0 \\ N_1 \\ N_2 \\ N_{ad} \end{pmatrix}_t, \qquad t = 1990, \ldots, 2015$$

3.2.2. *Demographic information*

In this subsection, we describe how to estimate fecundity, calf survival, adult survival and sex ratio using the data described in Section 2.

3.2.2.1. Estimation of Fecundity

We have data, J_t and R_t, which are obtained by radio collar tracking. These represent the number of parturient females that are 36 months or older and the number of cows that are 36 months or older, respectively. We choose a Binomial distribution to estimate the fecundity (f_t), using the data from the radio collared study, consisting of the number of adult females 36 months or older that had been radio collared (R_t) and the number that are parturient among them (J_t).

$$J_t \sim \text{Binomial}(\ R_t\ ,\ f_t\ ), \qquad t = 1990, \ldots, 2016$$

We assume independent Beta(a , b) distributions for f_t, where the hyperpriors for a and b are chosen so that the mean and the variance of f_t are approximately equal to those of

J_t/R_t, which are 0.825 and 0.013 based on 27 years of data.

3.2.2.2. Estimation of Adult Female Survival Probability

$SSad_t$ and Sad_t denote the number of at-risk and the number of surviving cows, respectively, which we obtained from the survival study. In other words, there are $SSad_t$ many collared cows in the summer of year t, and Sad_t many of them survived for at least a year from that time. A Binomial distribution is applied to model the adult female survival probability (ϕad_t).

$$Sad_{t+1} \sim \text{ Binomial}(\ SSad_t\ ,\ \phi ad_t\ ), \qquad\qquad t = 1991, \ldots, 2015$$

The survival probability, (ϕad_t) is given a Beta($a.ad$, $b.ad$) distribution, where $a.ad$ and $b.ad$ were chosen so that the mean and the variance of ϕad_t is approximately 0.914 and 0.00167, which is consistent with a crude estimate of survival probability from the raw dataset (n=26 years).

3.2.2.3. Estimation of Calf Survival Probability in their First 12 months

Our calf survival model is constructed similarly to adult female survival, except that the available dataset is limited from 1994 through 2002. Here, $SS01_t$ and $S01_t$ indicate the number of at-risk and the number of surviving calves, respectively. The number of surviving calves ($S01_{t+1}$) follows a Binomial distribution with the number of calves that were born in the year before ($SS01_t$), and the survival probability ($\phi 01_t$).

$$S01_{t+1} \sim \text{ Binomial}(\ SS01_t\ ,\ \phi 01_t\ ), \qquad\qquad t = 1994, \ldots, 2002$$

The survival probability ($\phi 01_t$) is given a Beta($a01$, $b01$) distribution, where $a01$ and $b01$ are chosen so that the mean and the variance of $\phi 01_t$ is approximately 0.518 and 0.0101, to be consistent with a crude estimate of survival probability ($S01/SS01$) from the raw dataset (n=9 years). This prior distribution of $\phi 01_t$ is used with other linked information to impute the calf survival probability for years with no survival data.

3.2.2.4. Estimation of Population Size

We chose the prior mean population size of each age group for the initial year of the study period based on the census counts and assumed that the actual initial population size is normally distributed with a relatively large variance in order to let the model provide actual estimates. For the initial year, which is 1990, we use a normal distribution based on the minimum photo census counts and the sex and calf-to-adult ratio. That is, we set the mean of the distribution as 4000, 3000, 2000, and 2000 for $N_{0,1}$, $N_{1,1}$, $N_{2,1}$, and $N_{ad,1}$, respectively. The standard deviation 3000 was given to them uniformly. The distribution of each age-group population for the second year and after are chosen as follows, based on the relationship of parameters as explained in Section 3.2.1.

$$N_{0,t+1} \sim \text{Poisson}(\ \phi ad_t \cdot \tfrac{f_{t+1}}{2} \cdot N_{ad,t}\ ), \qquad t = 1991, \ldots, 2015$$
$$N_{1,t+1} \sim \text{Binomial}(\ N_{0,t}\ ,\ \phi 01_t\ ), \qquad t = 1991, \ldots, 2015$$
$$N_{2,t+1} \sim \text{Binomial}(\ N_{1,t}\ ,\ \phi_{12,t}\ ), \qquad t = 1991, \ldots, 2015$$
$$N_{ad,t+1} \sim \text{Binomial}(\ N_{2,t} + N_{ad,t}\ ,\ \tfrac{N_{2,t} \cdot \phi 23_t + N_{ad,t} \cdot \phi ad_t}{N_{2,t} + N_{ad,t}}\ ), \qquad t = 1991, \ldots, 2015$$

Binomial distributions are used for the 12 months or older age groups, because they have hard upper bounds; for example, the population size of 12 months old at year $t + 1$ cannot be 5000 if the population size of 0 months old at year t is 4000. Each individual that is 0 months old at year t has a probability of $\phi 01_t$ becoming 12 months old in the following year. On the other hand, the number of newborns does not have a hard upper bound, so we use a Poisson distribution.

3.2.2.5. Estimation of Adult Sex Ratio

We include adult sex ratio information in our estimate of N_t to account for all caribou, not just the females. The number of females that are 12 months or older (Cf_t) and the number of adults (Cad_t) are used for estimating the sex ratio. We assumed Cf_t has a Binomial distribution,

$$Cf_t \sim \text{Binomial}(\ Cad_t\ ,\ FM_t\ ), \qquad t = 1990, \ldots, 2015$$

where FM_t is the probability that a randomely selected caribou is a female. FM_t is given a Beta($a.comp$, $b.comp$) distribution, where the distribution of hyperpriors $a.comp$ and *b.comp* are chosen so that the mean and the variance of FM_t are approximately 0.724 and 0.0065, which is consistent with a crude estimate of the fraction of females in the population (n=26 years).

3.2.3. *Integration of the model*

Our study years are from 1990 through 2016. Within these years, we have 12 years of count estimate data; the details were given in the data section. These count estimates are linked to the true latent population at year t (N_t). $Ntot$, the total population including calves, adult males and females, is derived using N's, sex ratio, and early survival probability of newborn calves. In FCH, there is no evidence for different survival probabilities between males and females, either for their first four months or one year of age (Boertje et al, 2017); thus the population of 12 months old is $2 \times N1$. When referring to the N's, a year "starts" when the calves are born, which is from mid- to the end of May. This is two to four weeks earlier than the photos that were taken for obtaining the minimum count. The calf survival probability for this brief period of time is about 0.724 and the variance 0.00645 among different years, based on the available data. We use the mean as a fixed early-survival probability, because the variability among years is small. We assume that the adult survival probability during this period is high enough that the estimates, N_{ad}'s do not need to be adjusted. Our sex composition model gives us the estimated proportion of females among the total adult population, where adult means 12 months or older. Hence, the total population size of 12 months or older animals is $(N_1 + N_2 + N_{ad})/FM$.

$$\mathbb{E}(N_{tot,t+1}) = 2 \times 0.724 \times N_{0,t} + (N_{1,t} + N_{2,t} + N_{ad,t})/FM_t \ , \qquad t = 1990, \ldots, 2015$$

We assume that the census counts, which are lower bounds for the population size, have a half-normal distribution with the maximum, $Ntot$. That is,

$$y_t \sim f(\ \cdot\ ;\ \sigma_y^2\ ,\ N_{tot,t})\ ,\ \text{where}\ f(y_t\ ;\ \sigma_y^2\ ,\ N_{tot,t}) = \frac{2}{\sqrt{2\pi\sigma_y^2}} \cdot \exp\left(-\frac{1}{2\sigma_y^2}(y_t - N_{tot,t})^2\right) I(y_t \le N_{tot,t}),$$
$$t = 1990, 1992, 1994, \ldots, 2000, 2003, 2009, 2010$$

We use a Uniform(0, 3000) prior distribution for σ_y.

Figure 4 summarizes our IPM, where we integrated the three factors described in the subsections above.

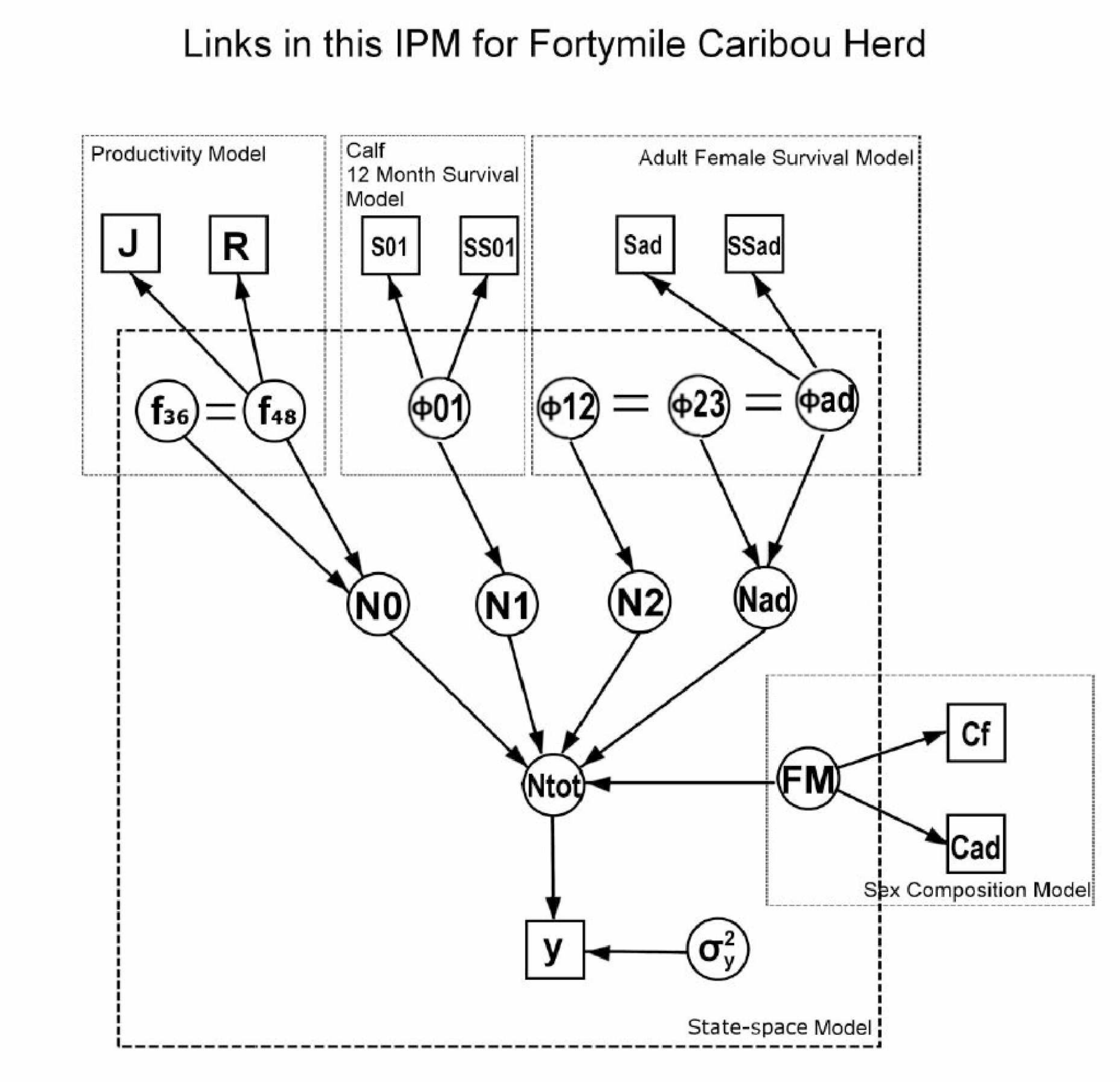

Figure 4.

.

The integrated model likelihood function is:

$L(\boldsymbol{y}, \boldsymbol{S}01, \boldsymbol{Sad}, \boldsymbol{J}, \boldsymbol{R}, \boldsymbol{Cf}, \boldsymbol{Cad} \mid \boldsymbol{N}_0, \boldsymbol{N}_1, \boldsymbol{N}_2, \boldsymbol{N}_{ad}, \boldsymbol{\phi}01, \boldsymbol{\phi ad}, \boldsymbol{FM}, \sigma_y^2)$

$= L(\boldsymbol{y} \mid \boldsymbol{N_{tot}}, \sigma_y^2)L(\boldsymbol{S}01 \mid \boldsymbol{\phi}01)L(\boldsymbol{Sad} \mid \boldsymbol{\phi ad})L(\boldsymbol{J} \mid \boldsymbol{f})L(\boldsymbol{N_{tot}} \mid \boldsymbol{N}_0, \boldsymbol{N}_1, \boldsymbol{N}_2, \boldsymbol{N}_{ad}, \boldsymbol{FM})$

The joint posterior distribution is:

$$P(\boldsymbol{N_0}, \boldsymbol{N_1}, \boldsymbol{N_2}, \boldsymbol{N_{ad}}, \boldsymbol{\phi 01}, \boldsymbol{\phi ad}, \boldsymbol{f}, \boldsymbol{FM}, \sigma_y^2 \mid \text{data})$$

$$\propto L(\boldsymbol{y} \mid \boldsymbol{N_{tot}}\ ,\ \sigma_y^2) \qquad \text{Normal}(\ N_t\ ,\ \sigma_y^2\ ) \text{ or Normal}(\ N_t\ ,\ \sigma_y^2\ ) \text{ truncated at } y_t$$

$$\times L(\boldsymbol{S01}\ ,\ \boldsymbol{SS01} \mid \boldsymbol{\phi 01}) \qquad S01_{t+1} \sim \text{Binomial}(\ SS01_t\ ,\ \phi 01_t\ )$$

$$\times L(\boldsymbol{Sad}\ ,\ \boldsymbol{SSad} \mid \boldsymbol{\phi ad}) \qquad Sad_{t+1} \sim \text{Binomial}(\ SSad_t\ ,\ \phi ad_t\ )$$

$$\times L(\boldsymbol{J}\ ,\ \boldsymbol{R} \mid \boldsymbol{f}) \qquad J_{t+1} \sim \text{Binomial}(\ R_t\ ,\ f_t\ )$$

$$\times L(\boldsymbol{N} \mid \boldsymbol{\phi 01}\ ,\ \boldsymbol{\phi ad}\ ,\ \boldsymbol{f}) \qquad N_{0,t+1} \sim \text{Poisson}\left(\ \phi ad_t \cdot \frac{f_{t+1}}{2} \cdot N_{ad,t}\right)$$

$$N_{ad,t+1} \sim \text{Binomial}\left(N_{2,t} + N_{ad,t}\ ,\ \frac{N_{2,t} \cdot \phi 23_t + N_{ad,t} \cdot \phi ad_t}{N_{2,t} + N_{ad,t}}\right)$$

$$\times L(\boldsymbol{Cf}\ ,\ \boldsymbol{Cad} \mid \boldsymbol{FM}) \qquad Cf_t \sim \text{Binomial}(\ Cad_t\ ,\ FM_t\ )$$

$$\times \pi(\boldsymbol{\phi 01}) \qquad \phi 01_t \sim \text{Beta}(\ a01\ ,\ b01\ )$$

$$\times \pi(\boldsymbol{\phi ad}) \qquad \phi ad_t \sim \text{Beta}(\ a.ad\ ,\ b.ad\ )$$

$$\times \pi(\boldsymbol{f}) \qquad f_t \sim \text{Beta}(\ a\ ,\ b\ )$$

$$\times \pi(\boldsymbol{FM}) \qquad FM_t \sim \text{Beta}(\ a.comp\ ,\ b.comp\ )$$

$$\times \pi(\sigma_y)$$

$$\times \pi(a)\pi(b)$$

$$\times \pi(a.ad)\pi(b.ad)$$

$$\times \pi(a01)\pi(b01)$$

$$\times \pi(a.comp)\pi(b.comp)$$

3.2.4. *Fitting the Model*

The program Jags, called through the R package R2jags (Su and Yajima, 2015), was used to generate the Markov chain Monte Carlo (MCMC) samples that are used to explore the joint posterior distribution of the parameters. First, we ran 100,000 iterations with 3 chains, and kept every 20th iteration to obtain trace plots. The results show that the MCMC for most parameters converges after about 15,000 iterations. Hence, for the analysis we run 1,025,000 iterations with 3 chains; the first 25,000 are discarded as burn-in, while the rest of the iterations are thinned by a factor of 50. We note that the traceplots for some parameters are somewhat problematic, but were considered acceptable.

3.2.5. *Sensitivity Analysis: Selecting higher prior variance for the state vectors*

We allow for larger observation errors by doubling the range of the σ_y from between 0 and 3000 to between 0 and 6000 to see the effects on our estimates.

4. Results

4.1. **Model Fit**

Our IPM smooths the population growth estimates from 2004 through 2008 as expected (Appendix B-1A). Our IPM estimates for those years with census counts data reflect adult female survival probabilities and their productivity. For example, the drop of population size estimates in 2005 and 2006 are likely the result of the low productivity in 2005 and 2006, and the low adult survival probability in 2004 and 2005. Another example of a drop in the population estimate is shown in 2014, which reflected the low productivity in 2014. The vertical red lines on the plot of IPM population estimates in Appendix B-1A indicate 95% credible intervals. The credible interval for the population size becomes wider as it gets farther from a year with an observed count y_t. Most of the counts y_t are within the credible interval for N's except for 2009. In Appendix B-1B, we calculate values that help us see whether the credible intervals are wide relative to the estimated population size. To be specific, we divide half of the width of credible interval by the mean of the estimates for the year.

The estimate of calf survival probability for 13 consecutive years from 2003 through 2015 borrows information about survival from the years that had data (Appendix B-2). The credible intervals of $\phi 01$ are wide, regardless of the number of consecutive years without data. As seen in Appendix B-2, the estimate of $\phi 01$ for 2009 jumps up. This is a result of calf survival data being the only type of data that is missing for the years 2009 and 2010. In other words, this survival estimate is determined to be the most plausible probability for population size to be close to the observed count for 2010. The plots of adult female survival probability shown in appendix B-3 has a typical smoothing feature compared to the plots of $Sad/SSad$. All the parameter estimates from the demographic data (survival probabilities and productivity) are within the corresponding credible intervals we obtained from our MCMC.

All the posterior distributions of parameters are smooth and unimodal. It should be mentioned that the right-skewed posterior distribution of the total population parameter ($N_{tot,t}$) for years with data is a consequence of the fact that y_t is a minimum count. In other words, $N_{tot,t}$ has to be greater than y_t (Appendix C).

Appendix D summarizes the results of MCMC with the mean of each posterior distribution, 95% credible interval, the potential scale reduction factor ($\hat{R}$), and an estimate of the effective sample size (n.eff) for each parameter. All the effective sample sizes are 490 or greater, and all $\hat{R}$'s are smaller than 1.05, which suggests that the MCMC has converged.

The model running time was 8036 seconds (two hours 14 minutes), using a Dell laptop with Intel-Core i3 CPU (1.90 GHz).

4.2. **Selecting higher prior variance for the state vectors**

Allowing a greater range of observation error for y's shifted our estimates of N_{tot}'s higher overall. A comparison of the estimates between the two models with different observation error ranges are shown in Appendix B-1.

5. Conclusions

FCH has been studied sufficiently for us to construct a properly structured IPM. We obtained estimates of the population size for those years with no aerial photo census, using limited data collected in multiple separate studies. The uncertainty of the population size estimate becomes larger as it gets farther from either the last year with the observed count y_t before the year of the estimation, or the first year with y_t after the year of the estimation. It is necessary to have some sort of count data obtained by a consistent method to be used as an index, which we discuss in the next section. The possible use of a stochastic model in an integrated model, which reflects the population dynamics in the real world, was demonstrated, though there are more studies to be done, which we discuss in the next section.

6. Discussion

One of the studies that should be considered in the future concerns sample size. For example, our calf survival dataset size is limited to nine years. The jump we see in the 2009 estimate of $\phi 01$ is due to the existence of census counts following five years of no census count. That is, our estimates of the calf survival probabilities after 2003 are not meaningful. The appropriate amount of data for estimating certain parameters from the IPM is difficult to determine, because it depends on the amount of other types of data as well. The more types of available data we have, the better link an IPM could build. Additionally, the amount of missing information in a year influences the uncertainty of the estimates. The combination of all four types of data - count data, adult female survival data, calf survival data, and parturition data from 1994 through 2000 - helped estimate relationships among the parameters. However, two types of parameters (count data and calf survival data) being missing from 2004-2008 and 2011-2014 lead to (1) the wide credible interval for calf survival estimates and (2) the higher estimates of adult female survival probabilities having a larger weight than they are supposed to.

The credible interval of our IPM estimates of the N_{tot}'s for those years with census count data are somewhat narrower than we expected. Nevertheless, the half-width of the credible intervals are still roughly 5% of the estimated population size. We fitted the model with two different value for the upper limit of σ_y and saw the upward shift of N_{tot} estimates of all the years. Even larger values should be tested to find the upper limit of σ_y to see where the upward shift stops.

Sensitivity of results to the choice of prior distribution is something that needs to be studied in the future. When we have small datasets, the prior distribution heavily influences the posterior distribution. For example, we use a Poisson distribution for the prior of $N_{0,t}$

in our model. It would be interesting to see how it would affect the results when a Binomial distribution is used. One important thing that wildlife managers need to keep in mind is that the estimate for "missing data" in the past could change every time we obtain new data. In other words, a Bayesian IPM improves an estimate of a parameter when there are more available combinations of data. Finding an appropriate observation error range for y's could be challenging because we will never know the actual population size. Finding the true population size may not be necessary, though we should keep it in mind that it affects the estimation of missing data. Setting appropriate margins of error is critical so that wildlife managers could make decisions appropriately for maintaining a sustainable population size and for the public understanding of change that could happen in the future. Another thing to be studied is how we can estimate parameters if we have any missing data in a year with a big event such as wildfire. Additionally, the history of the population size change in the herd shows a large fluctuation. There may be other environmental factors that need to be taken into account if a long-term projection is attempted.

Our model was fairly simple as far as the number of the types of data. We could improve our estimates by including other types of data. Additional generally-available data is harvest data. Moreover, the harvested number is one of the most precise data types that is available at no cost. Although survival data is affected by the mortality caused by humans, we believe there is association between human caused mortality and other mortality in terms of location, season, and the health condition of the target individual. As far as parturition data, we have an average of 50.7 cows of 48 months old or older each year with the mean of $Sad_{t+1}/SSad_t$ being 85.1%, and the standard deviation 8.5%. On the other hand, our data for 36 months old include an average of 9.75 cows each year; and the mean of $Sad_{t+1}/SSad_t$ is 67.1%, and the standard deviation is 23.9%. Another model that separates age groups is worth attempting, even though a larger sample size for parturition probability that only consists of 36 month old cows is ideal. Particularly, with the recent range expansion and concerns about their nutritional condition, we suggest that a study on parturition probability of 36 months old cows be considered. The sex ratio of newborn calves or the weight of calves, which depends on the herd condition, could be another potential parameter that could be incorporated in this model. The IPM used in this study was shown to incorporate different types of data successfully and the inclusion of additional parameters warrants exploration.

The output of our model includes a large amount of information. Although the application of an IPM requires sensitivity analyses, an IPM was proven to be a valuable method to compensate for missing data that other methods could not have achieved. We hope this study will be used as an initial point of an IPM application to FCH management and beyond.

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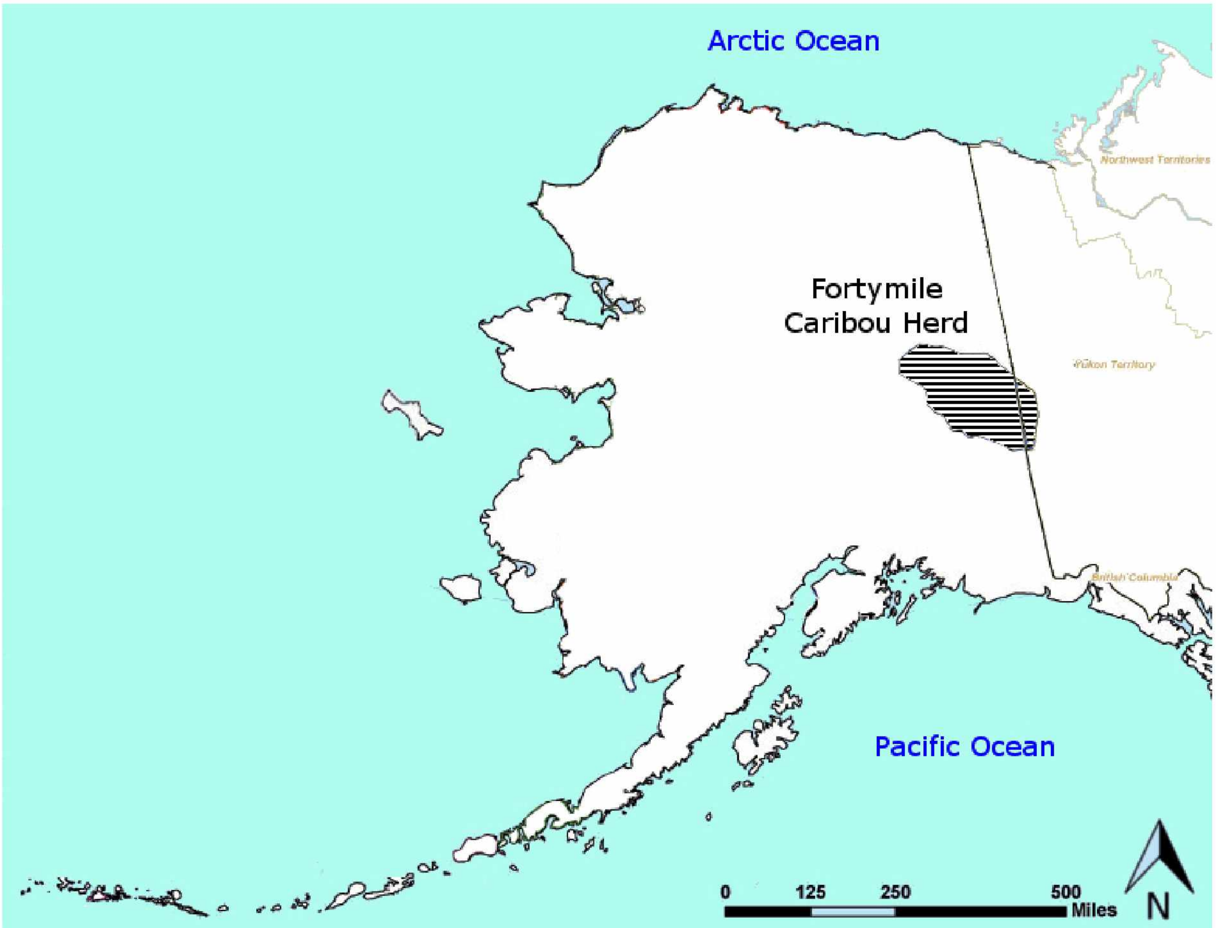
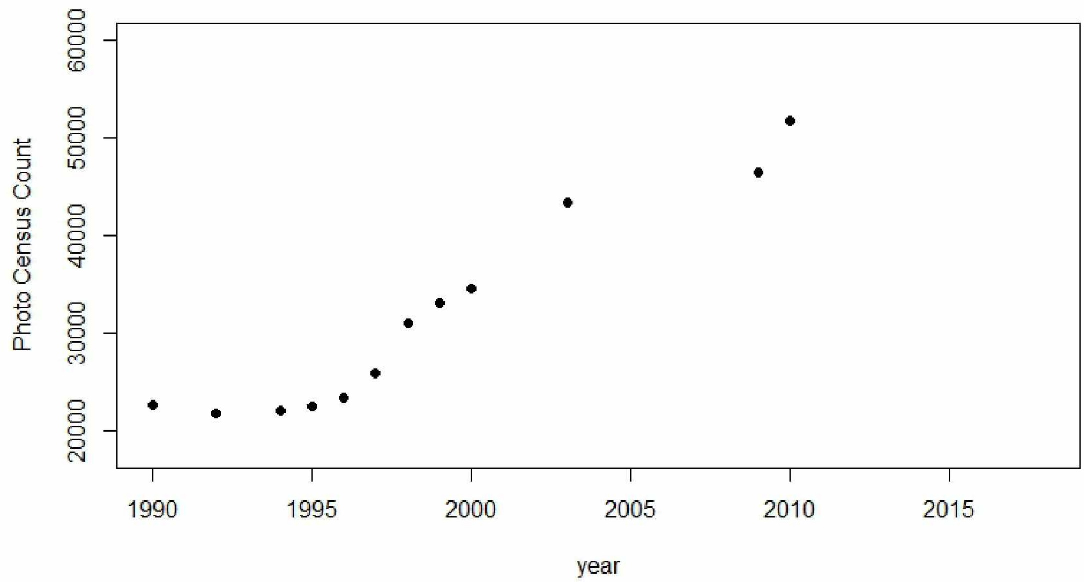
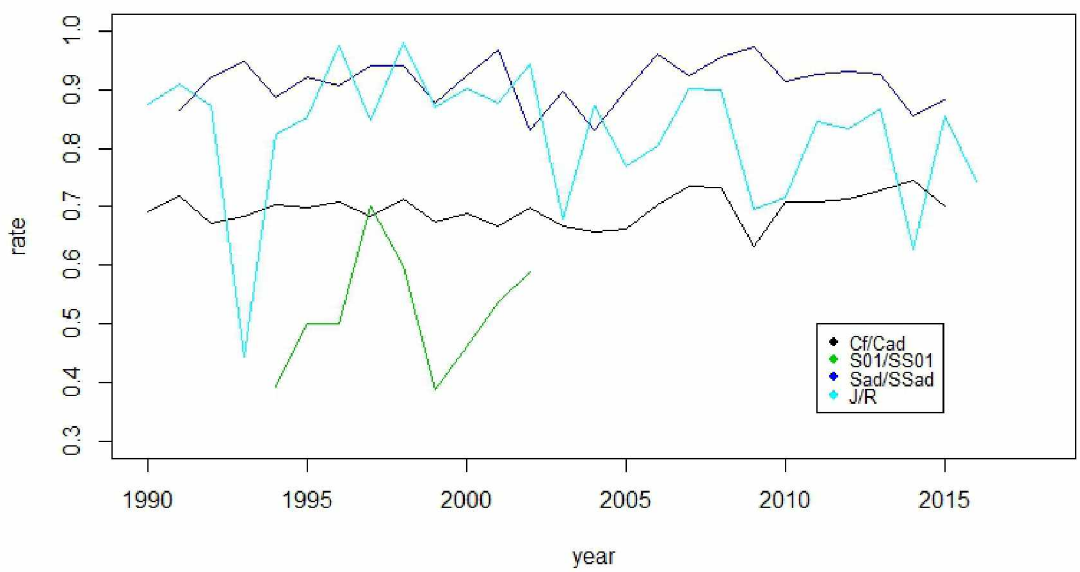
Appendix A -1 : Home Range of Fortymile Caribou Herd



(map reference : ADF&G website)

Appendix A -2 : Data Plots





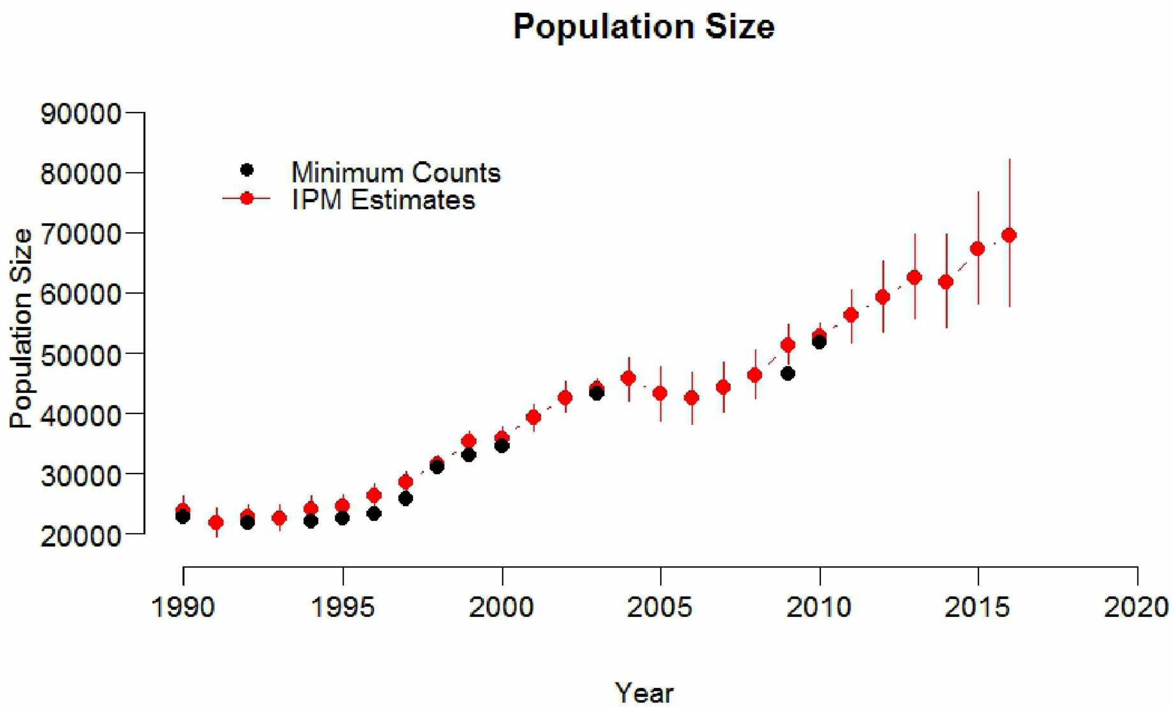
Cf/Cad: cow / (cow+bull) (12 months or older)

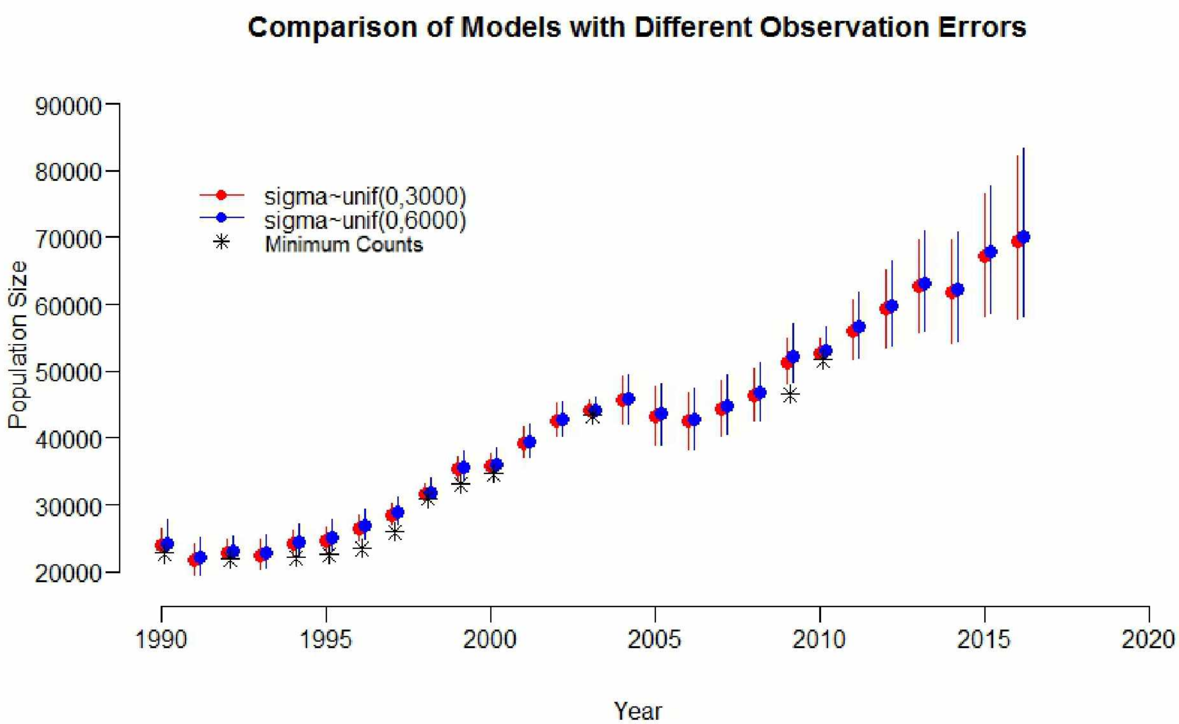
S01/SS01: # of survived yearling / # of new born calf

Sad/SSad: # of survived adult female / # of risk (12 months or older)

J/R: parturition / # of sampled cow (36 months or older)

Appendix B-1A : Comparison between counts estimates and IPM estimates





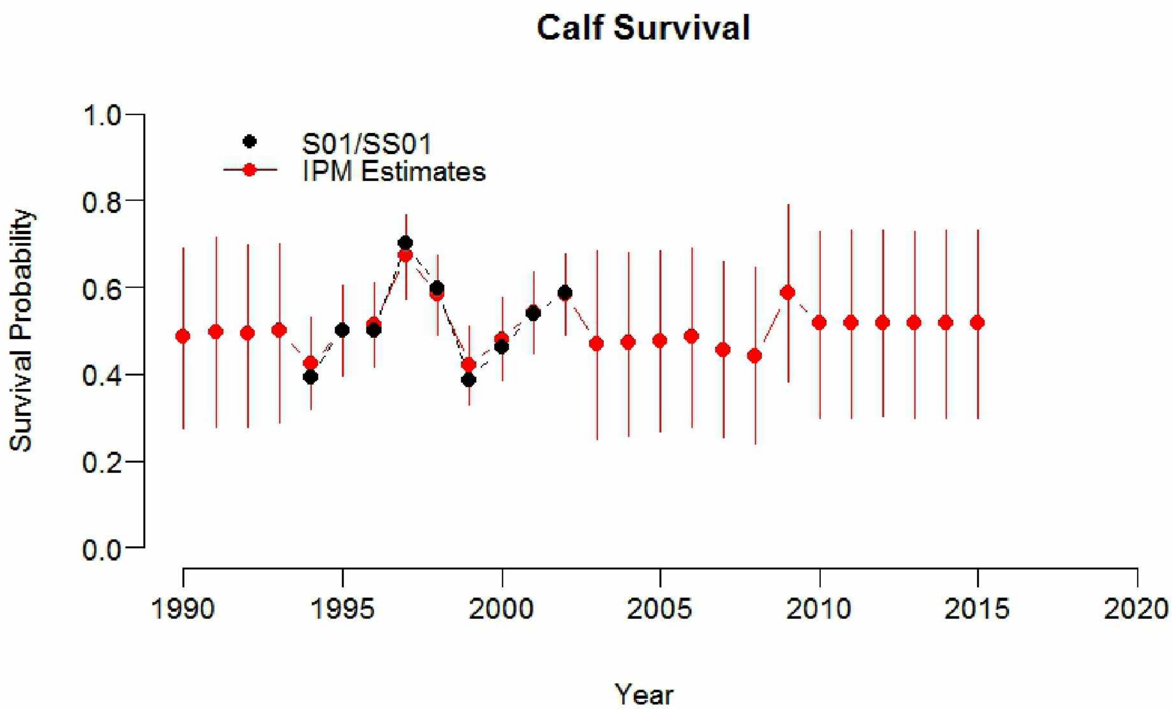
The blue plots are shifted slightly to the right so that they are easily compared with red plots. There is no temporal difference between red and blue.

Appendix B-1B : Comparison between counts estimates and IPM estimates

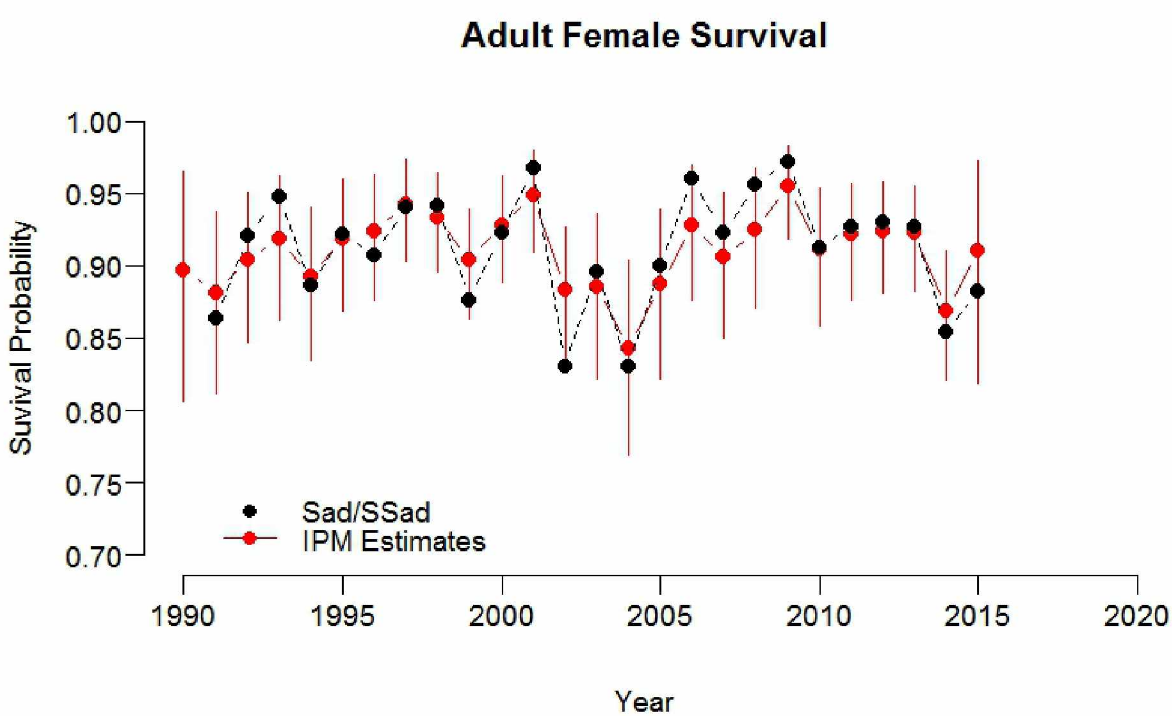
Proportion of the credible interval for the mean population estimate $N_{tot,t}$.

year	mean	(2.5% , 97.5%)	$\frac{cred.int.width}{mean \times 2}$ (%)	census data
1990	24000	(22800 , 26400)	7.5	yes
1991	21700	(19500 , 24300)	11.1	no
1992	22900	(21900 , 24900)	6.6	yes
1993	22500	(20500 , 24900)	9.8	no
1994	24100	(22400 , 26200)	7.9	yes
1995	24600	(22900 , 26700)	7.7	yes
1996	26500	(24700 , 28400)	7.0	yes
1997	28500	(27100 , 30200)	5.4	yes
1998	31700	(31000 , 33100)	3.3	yes
1999	35300	(33700 , 37200)	5.0	yes
2000	35900	(34700 , 37700)	4.2	yes
2001	39200	(37200 , 41600)	5.6	no
2002	42600	(40400 , 45200)	5.6	no
2003	44100	(43400 , 45800)	2.7	yes
2004	45700	(42100 , 49300)	7.9	no
2005	43300	(38900 , 47700)	10.2	no
2006	42500	(38300 , 46800)	10.0	no
2007	44400	(40400 , 48600)	9.2	no
2008	46300	(42600 , 50400)	8.4	no
2009	51300	(48200 , 54800)	6.4	yes
2010	52600	(51700 , 54900)	3.0	yes
2011	56100	(51700 , 60600)	7.9	no
2012	59300	(53500 , 65100)	9.8	no
2013	62600	(55800 , 69600)	11.0	no
2014	61800	(54200 , 69600)	12.5	no
2015	67100	(58200 , 76600)	13.7	no
2016	69500	(57700 , 82100)	17.6	no

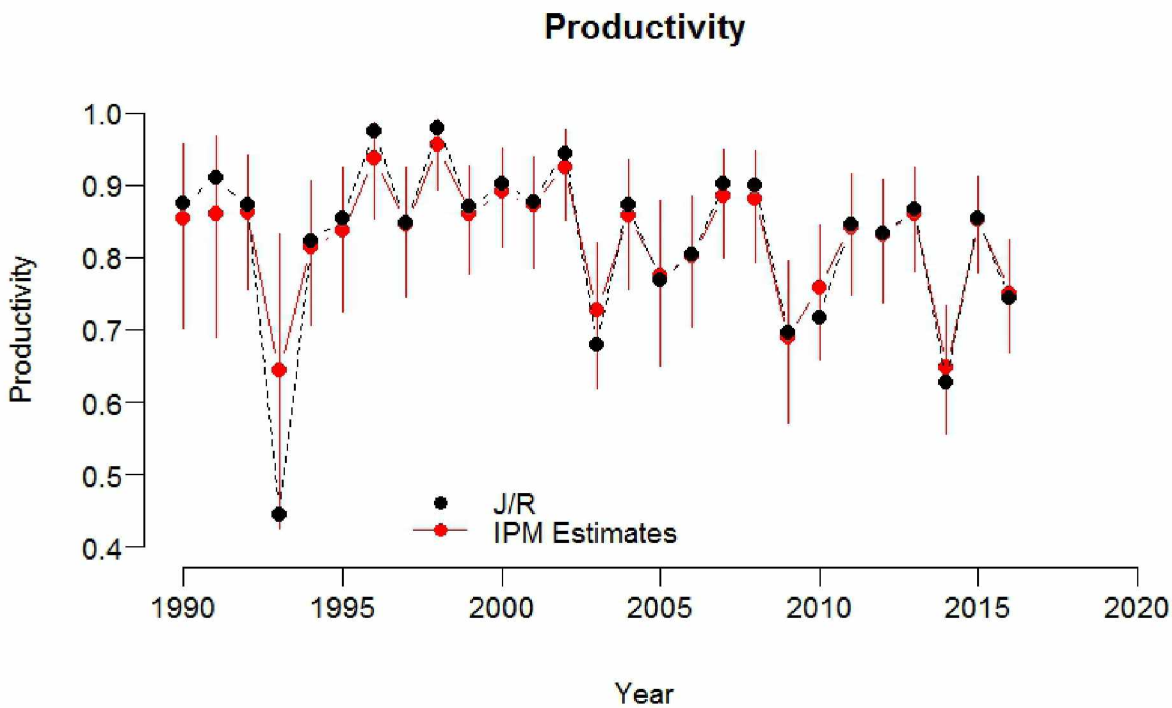
Appendix B-2 : Calf Survival Probability from Data and those with IPM estimates



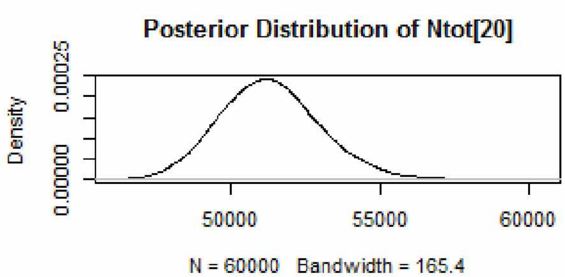
Appendix B-3 : Adult Female Survival Probability from Data and those with IPM estimates

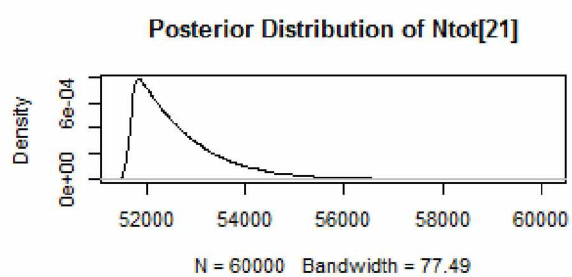


Appendix B-4 : Productivity from Data and those with IPM estimates



Appendix C : Examples of Posterior Distribution (total female population for year 2009 and 2010) showing the result using non-truncated and truncated normal as a prior distribution (iteration: 1025000, thinned by 50, burn-in: 25000, number of chain: 3)





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Appendix D. Summary Table

Inference for Bugs model at "ipm.jags", fit using jags, 3 chains, each with 1025000 iterations (first 25000 discarded), n.thin = 50, n.sims = 60000 iterations saved

For each parameter, n.eff is a crude measure of effective sample size, and Rhat is the potential scale reduction factor (at convergence, Rhat=1).

	mean	sd	2.5%	97.5%	Rhat	n.eff
FM[1]	6.92e-01	1.10e-02	6.70e-01	7.13e-01	1.00	56000
FM[2]	7.14e-01	1.14e-02	6.92e-01	7.36e-01	1.00	60000
FM[3]	6.74e-01	9.45e-03	6.55e-01	6.92e-01	1.00	26000
FM[4]	6.86e-01	8.02e-03	6.70e-01	7.02e-01	1.00	55000
FM[5]	7.04e-01	8.59e-03	6.87e-01	7.21e-01	1.00	60000
FM[6]	6.98e-01	8.34e-03	6.82e-01	7.14e-01	1.00	60000
FM[7]	7.09e-01	7.17e-03	6.95e-01	7.23e-01	1.00	25000
FM[8]	6.85e-01	6.45e-03	6.72e-01	6.97e-01	1.00	60000
FM[9]	7.11e-01	7.33e-03	6.96e-01	7.25e-01	1.00	36000
FM[10]	6.78e-01	7.55e-03	6.63e-01	6.92e-01	1.00	60000
FM[11]	6.90e-01	6.01e-03	6.78e-01	7.01e-01	1.00	18000
FM[12]	6.69e-01	6.16e-03	6.57e-01	6.81e-01	1.00	60000
FM[13]	6.99e-01	6.45e-03	6.87e-01	7.12e-01	1.00	60000
FM[14]	6.66e-01	6.05e-03	6.54e-01	6.78e-01	1.00	60000
FM[15]	6.60e-01	7.77e-03	6.45e-01	6.75e-01	1.00	60000
FM[16]	6.66e-01	9.64e-03	6.47e-01	6.85e-01	1.00	60000
FM[17]	7.03e-01	6.96e-03	6.89e-01	7.17e-01	1.00	60000
FM[18]	7.33e-01	6.66e-03	7.20e-01	7.46e-01	1.00	60000
FM[19]	7.30e-01	7.82e-03	7.15e-01	7.45e-01	1.00	60000
FM[20]	6.42e-01	8.03e-03	6.26e-01	6.58e-01	1.00	11000
FM[21]	7.08e-01	5.81e-03	6.96e-01	7.19e-01	1.00	37000
FM[22]	7.08e-01	7.50e-03	6.93e-01	7.23e-01	1.00	42000
FM[23]	7.12e-01	6.78e-03	6.99e-01	7.25e-01	1.00	27000
FM[24]	7.26e-01	7.49e-03	7.11e-01	7.41e-01	1.00	60000
FM[25]	7.43e-01	6.66e-03	7.29e-01	7.56e-01	1.00	46000
FM[26]	7.02e-01	6.54e-03	6.89e-01	7.15e-01	1.00	39000
FM[27]	6.96e-01	2.70e-02	6.42e-01	7.48e-01	1.00	60000
Ntot[1]	2.40e+04	9.89e+02	2.28e+04	2.64e+04	1.00	3800
Ntot[2]	2.17e+04	1.22e+03	1.95e+04	2.43e+04	1.00	7800
Ntot[3]	2.29e+04	8.07e+02	2.19e+04	2.49e+04	1.00	4200

Ntot[4]	2.25e+04	1.12e+03	2.05e+04	2.49e+04	1.00	1000
Ntot[5]	2.41e+04	9.94e+02	2.24e+04	2.62e+04	1.00	540
Ntot[6]	2.46e+04	9.72e+02	2.29e+04	2.67e+04	1.00	610
Ntot[7]	2.65e+04	9.46e+02	2.47e+04	2.84e+04	1.00	2000
Ntot[8]	2.85e+04	8.15e+02	2.71e+04	3.02e+04	1.00	3600
Ntot[9]	3.17e+04	5.59e+02	3.10e+04	3.31e+04	1.00	7200
Ntot[10]	3.53e+04	8.92e+02	3.37e+04	3.72e+04	1.00	2400
Ntot[11]	3.59e+04	8.12e+02	3.47e+04	3.77e+04	1.00	16000
Ntot[12]	3.92e+04	1.12e+03	3.72e+04	4.16e+04	1.00	4800
Ntot[13]	4.26e+04	1.23e+03	4.04e+04	4.52e+04	1.00	4100
Ntot[14]	4.41e+04	6.60e+02	4.34e+04	4.58e+04	1.00	9400
Ntot[15]	4.57e+04	1.85e+03	4.21e+04	4.93e+04	1.00	16000
Ntot[16]	4.33e+04	2.25e+03	3.89e+04	4.77e+04	1.00	8400
Ntot[17]	4.25e+04	2.17e+03	3.83e+04	4.68e+04	1.00	2600
Ntot[18]	4.44e+04	2.10e+03	4.04e+04	4.86e+04	1.00	1200
Ntot[19]	4.63e+04	1.99e+03	4.26e+04	5.04e+04	1.00	3200
Ntot[20]	5.13e+04	1.66e+03	4.82e+04	5.48e+04	1.00	31000
Ntot[21]	5.26e+04	8.61e+02	5.17e+04	5.49e+04	1.00	20000
Ntot[22]	5.61e+04	2.25e+03	5.17e+04	6.06e+04	1.00	60000
Ntot[23]	5.93e+04	2.97e+03	5.35e+04	6.51e+04	1.00	60000
Ntot[24]	6.26e+04	3.51e+03	5.58e+04	6.96e+04	1.00	60000
Ntot[25]	6.18e+04	3.94e+03	5.42e+04	6.96e+04	1.00	60000
Ntot[26]	6.71e+04	4.67e+03	5.82e+04	7.66e+04	1.00	60000
Ntot[27]	6.95e+04	6.20e+03	5.77e+04	8.21e+04	1.00	60000
deviance	7.28e+02	1.32e+01	7.04e+02	7.56e+02	1.00	8900
f[1]	8.53e-01	6.64e-02	7.01e-01	9.57e-01	1.00	60000
f[2]	8.60e-01	7.28e-02	6.90e-01	9.69e-01	1.00	60000
f[3]	8.61e-01	4.77e-02	7.56e-01	9.41e-01	1.00	28000
f[4]	6.45e-01	1.04e-01	4.26e-01	8.32e-01	1.00	9500
f[5]	8.15e-01	5.13e-02	7.06e-01	9.05e-01	1.00	6400
f[6]	8.37e-01	5.14e-02	7.25e-01	9.25e-01	1.00	60000

f[7]	9.37e-01	3.48e-02	8.53e-01	9.87e-01	1.00	18000
f[8]	8.46e-01	4.60e-02	7.46e-01	9.25e-01	1.00	3300
f[9]	9.55e-01	2.55e-02	8.93e-01	9.91e-01	1.00	20000
f[10]	8.59e-01	3.85e-02	7.76e-01	9.26e-01	1.00	5700
f[11]	8.92e-01	3.51e-02	8.15e-01	9.51e-01	1.00	46000
f[12]	8.72e-01	3.96e-02	7.85e-01	9.38e-01	1.00	60000
f[13]	9.25e-01	3.18e-02	8.52e-01	9.75e-01	1.00	8900
f[14]	7.26e-01	5.20e-02	6.19e-01	8.21e-01	1.00	60000
f[15]	8.58e-01	4.59e-02	7.57e-01	9.34e-01	1.00	25000
f[16]	7.74e-01	5.86e-02	6.51e-01	8.78e-01	1.00	12000
f[17]	8.03e-01	4.63e-02	7.04e-01	8.85e-01	1.00	35000
f[18]	8.85e-01	3.81e-02	8.00e-01	9.48e-01	1.00	19000
f[19]	8.81e-01	3.92e-02	7.94e-01	9.46e-01	1.00	60000
f[20]	6.90e-01	5.77e-02	5.72e-01	7.96e-01	1.00	4300
f[21]	7.58e-01	4.77e-02	6.59e-01	8.45e-01	1.00	60000
f[22]	8.41e-01	4.39e-02	7.47e-01	9.16e-01	1.00	60000
f[23]	8.31e-01	4.39e-02	7.37e-01	9.08e-01	1.00	37000
f[24]	8.60e-01	3.71e-02	7.80e-01	9.25e-01	1.00	60000
f[25]	6.47e-01	4.48e-02	5.57e-01	7.32e-01	1.00	41000
f[26]	8.51e-01	3.42e-02	7.78e-01	9.12e-01	1.00	60000
f[27]	7.51e-01	3.99e-02	6.69e-01	8.25e-01	1.00	60000
phi01[1]	4.87e-01	1.06e-01	2.75e-01	6.90e-01	1.00	4000
phi01[2]	4.96e-01	1.10e-01	2.79e-01	7.13e-01	1.00	13000
phi01[3]	4.92e-01	1.06e-01	2.80e-01	6.97e-01	1.00	22000
phi01[4]	4.99e-01	1.05e-01	2.89e-01	7.02e-01	1.00	12000
phi01[5]	4.24e-01	5.41e-02	3.19e-01	5.30e-01	1.00	3000
phi01[6]	4.99e-01	5.31e-02	3.96e-01	6.04e-01	1.00	3400
phi01[7]	5.14e-01	4.95e-02	4.18e-01	6.11e-01	1.00	1800
phi01[8]	6.73e-01	4.97e-02	5.73e-01	7.67e-01	1.00	1800
phi01[9]	5.83e-01	4.65e-02	4.91e-01	6.73e-01	1.00	6800
phi01[10]	4.19e-01	4.55e-02	3.31e-01	5.09e-01	1.00	900

phi01[11]	4.81e-01	4.91e-02	3.85e-01	5.78e-01	1.00	4400
phi01[12]	5.42e-01	4.78e-02	4.48e-01	6.35e-01	1.00	4700
phi01[13]	5.84e-01	4.76e-02	4.90e-01	6.76e-01	1.00	2000
phi01[14]	4.68e-01	1.09e-01	2.50e-01	6.82e-01	1.00	6400
phi01[15]	4.72e-01	1.07e-01	2.57e-01	6.78e-01	1.00	6200
phi01[16]	4.77e-01	1.06e-01	2.67e-01	6.82e-01	1.00	24000
phi01[17]	4.88e-01	1.04e-01	2.80e-01	6.89e-01	1.00	1400
phi01[18]	4.56e-01	1.03e-01	2.54e-01	6.59e-01	1.00	1100
phi01[19]	4.42e-01	1.04e-01	2.40e-01	6.45e-01	1.00	2300
phi01[20]	5.85e-01	1.03e-01	3.84e-01	7.89e-01	1.00	3500
phi01[21]	5.17e-01	1.09e-01	2.99e-01	7.30e-01	1.00	60000
phi01[22]	5.17e-01	1.09e-01	3.00e-01	7.30e-01	1.00	43000
phi01[23]	5.18e-01	1.09e-01	3.02e-01	7.31e-01	1.00	60000
phi01[24]	5.17e-01	1.08e-01	2.99e-01	7.28e-01	1.00	60000
phi01[25]	5.17e-01	1.09e-01	2.99e-01	7.31e-01	1.00	60000
phi01[26]	5.18e-01	1.09e-01	3.01e-01	7.32e-01	1.00	49000
phiad[1]	8.97e-01	4.12e-02	8.06e-01	9.66e-01	1.00	5500
phiad[2]	8.82e-01	3.22e-02	8.12e-01	9.37e-01	1.00	4900
phiad[3]	9.04e-01	2.67e-02	8.47e-01	9.51e-01	1.00	33000
phiad[4]	9.18e-01	2.56e-02	8.62e-01	9.62e-01	1.00	21000
phiad[5]	8.93e-01	2.71e-02	8.35e-01	9.41e-01	1.00	13000
phiad[6]	9.19e-01	2.33e-02	8.69e-01	9.60e-01	1.00	3000
phiad[7]	9.24e-01	2.23e-02	8.76e-01	9.63e-01	1.00	60000
phiad[8]	9.42e-01	1.82e-02	9.03e-01	9.73e-01	1.00	12000
phiad[9]	9.33e-01	1.75e-02	8.96e-01	9.64e-01	1.00	17000
phiad[10]	9.04e-01	1.94e-02	8.64e-01	9.39e-01	1.00	1100
phiad[11]	9.28e-01	1.90e-02	8.88e-01	9.62e-01	1.00	8800
phiad[12]	9.48e-01	1.82e-02	9.09e-01	9.80e-01	1.00	25000
phiad[13]	8.84e-01	2.41e-02	8.33e-01	9.27e-01	1.00	45000
phiad[14]	8.85e-01	2.92e-02	8.22e-01	9.36e-01	1.00	12000
phiad[15]	8.43e-01	3.44e-02	7.69e-01	9.04e-01	1.00	15000

phiad[16]	8.87e-01	3.01e-02	8.22e-01	9.39e-01	1.00	3600
phiad[17]	9.28e-01	2.40e-02	8.76e-01	9.69e-01	1.00	7800
phiad[18]	9.06e-01	2.56e-02	8.50e-01	9.51e-01	1.00	45000
phiad[19]	9.25e-01	2.47e-02	8.71e-01	9.67e-01	1.00	16000
phiad[20]	9.55e-01	1.67e-02	9.19e-01	9.83e-01	1.00	12000
phiad[21]	9.12e-01	2.44e-02	8.58e-01	9.54e-01	1.00	60000
phiad[22]	9.21e-01	2.09e-02	8.76e-01	9.57e-01	1.00	32000
phiad[23]	9.24e-01	1.96e-02	8.81e-01	9.57e-01	1.00	60000
phiad[24]	9.22e-01	1.86e-02	8.82e-01	9.55e-01	1.00	19000
phiad[25]	8.69e-01	2.28e-02	8.21e-01	9.10e-01	1.00	60000
phiad[26]	9.10e-01	3.94e-02	8.19e-01	9.72e-01	1.00	60000
sigma2.y	5.07e+06	2.10e+06	1.33e+06	8.74e+06	1.00	1700